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RESEARCH ARTICLE

Heterosis and inbreeding depression for yield and oil traits of sunflower genotypes under water stress conditions

Majid Hussain Kaleri[1], Wajid Ali Jatoi[1*], Munaiza Baoch [1] & Qamaruddin Chachar[2]

[1]Department of Plant Breeding and Genetics, Sindh Agriculture University, Tandojam-70060, Pakistan
[2]Department of Crop Physiology, Sindh Agriculture University, Tandojam-70060, Pakistan

*Email: jatoiwajid@yahoo.com

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Abstract

The mean squares from analysis indicated significant differences was observed between treatments, inbred parents, F_1 hybrids and F_2 progenies for agronomic, oil and protein traits. The noteworthy variances between parents vs. hybrids indicated the importance of heterosis breeding. heterotic effects were found as potential hybrids for earliness, seed yield, oil and protein content in both the environments. The hybrids such as Thatta × UC-666, Mehran × Peshawar-93 and HO.1 × B-2 which have articulated high hybrid vigor in F_1s for majority of the traits in normal and adverse conditions may be recommended for further commercial exploitation. The F_2 progenies manifested high inbreeding depression for phenological traits and plant height signified that earlier maturing and dwarf plants resistant to lodging can achieved from filial generations.

Keywords

Heterosis, inbreeding depression, water stress, yield and oil traits, sunflower genotypes

Introduction

The sunflower (*Helianthus annuus* L.) is one of the world's most important oilseed crops. Sunflower achene contains about 50% oil and 20-21 % protein that potentially fulfills the gap between global supply and consumption of sunflower as edible oil and animal feed purposes (1, 2). The traditional sunflower oil contains oleic acid, linoleic acid from 90% fatty acids while palmitic acid and stearic acid possess 8 to10% fatty acids (3). Ghee Corporation of Pakistan (GCP) pioneered the sunflower growing in Pakistan in 1980s (4). Drought is one of the most serious environmental factors that reduce 15 -20% sunflower yields (5). Drought stress requires an understanding of the nature of phenotypic traits that can recover the performance under water stress conditions as well as understanding of the complicated physiological and genetic mechanisms involved under stress conditions. In that context, one of the most important objectives of plant breeders is to improve drought tolerance and water productivity in plants for such areas. Taking into account the morphological, physiological, genetic and molecular pathways that influence drought tolerance can help evolve drought-tolerant cultivars for their cultivation in arid and semi-arid environments (6). Heterosis is defined as an increase or decrease in the vigour of F_1 hybrids as compared to its mid or better parental value. One of the objectives of such study was to determine the extent of heterosis for various attributes and to identify prospective hybrids for hybrids seed production and oil content over typical check hybrids for commercial exploitation (7). For this reason, sunflower breeding efforts are primarily focused on exploitation of heterosis, which has been shown as a viable tool for producing highly productive sunflower hybrids with agronomically superior features evolved from genetically diverse parents (8). Until now, there have been little efforts to select diversified superior inbreds in order to obtain higher level of heterosis over check hybrids. One of the practical uses of CMS research is the generation of CMS equivalent to B lines utilized in breeding of sunflower hybrid development (8). Growers were able to get larger number of seed and oil yields, as well as improved uniformity by manipulating heterosis for hybrid expansion (9). Sunflower is a highly cross-pollinated and perfect field crop for exploitation of heterosis. Discovery of cytoplasmic male sterility in sunflowers provided a breakthrough in heterosis breeding (10). Sunflower with high level of hybrid superiority in F_1 hybrids as well as its commercial application to adopt it has emerged as one of the world's most vital oil seed crops (11). Heterosis is closely linked to genetic differences across parental lines (12). Contrary to heterosis in F_1 hybrids, inbreeding depression is a classic phenomenon seen in F_2 hybrids, despite the superiority of F_1 hybrids over male and female inbred parents. It arises owing to homozygosity at several loci and is referred to as inbreeding depression. Apart from F_1, F_2 hybrids with more heterozygosity and genetic variability may have a wider range of adaption and better performance over their inbred parents or even over F_1 hybrids in some cases. In theory, F_2 populations should only display 50% of the economic heterosis seen in F_1 hybrids, and much less when heterosis is compared to a high yielding check. Nevertheless, in many crop species, F_2 hybrids with low inbreeding depression in yield and greater potential over cultivated varieties have been documented (13). Inbreeding depression or the decrease of fitness in performance caused by increased homozygozity can influence mating systems, dispersal strategies, and absolute fitness. It's not surprising that there have been so many empirical estimates of inbreeding depression (14). Plants exposed to new ecosystems or to new biotic and abiotic factors may also reduce their fitness. Long-distance dispersal is frequently associated with decreased fitness; therefore the early stages of adaptation may be stressful for many populations (15). Because they are not genetically adapted to such adverse conditions, inbred individuals may experience increased inbreeding depression when they disperse into new areas, and inbreeding depression can rise under stressful conditions (16). In F_1 hybrids, yield and leaf area showed considerable heterosis, whereas the F_2 population showed inbreeding depression (17).

Materials and Methods

The seeds of 5 CMS lines (HO-1, Mehran, Thatta, PSF-025, SH-3915) and 03 restorer (R) lines (UC-666, Peshawar-93, B-2) were obtained from Oil Seeds Research Institute, Tandojam tester parents which performed better in screening experiment were selected for crossing and genetic analysis. The seeds of 8 parents (5 lines and 03 testers) which were water stress tolerant were planted in a crossing block in lines × testers mating design. In the second experiment, the ability of CMS lines to combine with restorer testers, as well as their F_1 hybrids were assessed. Split plot design with 2 treatments (T_1= well watered and T_2= water stress at initial flowering to seed formation by stopping water in field conditions) in 4 replications. Water regimes were regarded as the most important component and in this they served as a main factor. Irrigation regimes with no water stress (well-watered) received frequent irrigations without any water stress, thus a total of 5 irrigations were applied, whereas water stress treatment received mild to severe stress imposed on 50-day-old plants near to flower bud until seed formation i.e. 80-day-old plants by withholding water for a period of 30 days. The data was examined for heterosis In third experiment, the F_2 populations were grown under well-watered and water stress condition for determining the inbreeding depression for days to seed formation, plant height (cm), seed yield kg ha^{-1}, Chlorophyll content, Linoleic acid, Oleic acid, Oil content, Protein content. The acquired data was subjected to analysis of variance using the statistical factorial plot model (18). Heterosis was calculated using method (19). Inbreeding depression was formulated as % decrease of F_2 populations by comparing with F_1 hybrid means (20).

Soil analysis and Meteorological data

Before conducting the experiment the following chemical properties of soil (Table 1) and meteorological data during the experiment (Table 2).

Table 1. Chemical properties of top soil layer and water at experimental site

Parameters	Soil	Water
Particle size distribution (%)		-
Sand	36.50	-
Silt	26.40	-
Clay	38.50	-
Textural class	Clay loam	-
Field capacity (%)	54.10	-
$CaCO_3$ (%)	6.30	-
Organic Matter (%)	0.58	-
pH (1:5)	7.70	7.50
EC (dS m^{-1})	1.20	2.00
Ca^{2+} (meq L^{-1})	3.80	4.00
Mg^{2+} (meq L^{-1})	1.90	2.30
Na^+ (meq L^{-1})	4.10	8.60
K^+ (meq L^{-1})	2.50	2.00
Cl^- (meq L^{-1})	5.00	9.00
SO_4^{2-} (meq L^{-1})	5.20	5.30

Table 2. Agro-meteorological data during 2019 to 2020

Year	Month	Rain fall	Temperature			R.H.*
		(mm)	Min. ^{0}C	Max. ^{0}C	Avg.	(%)
2019	January	0.00	13.80	32.60	23.20	54.00
	February	0.00	10.300	28.50	19.40	55.00
	March	0.06	17.30	32.10	24.70	60.00
	April	0.00	20.00	30.50	25.25	50.00
	May	0.00	25.50	40.50	33.00	46.00
	June	0.00	24.90	42.10	33.50	43.00
	July	0.00	25.60	45.70	35.65	50.00
	August	0.00	22.10	42.50	32.30	53.00
	September	0.80	20.00	38.50	29.25	50.00
	October	0.25	18.60	36.70	27.65	51.00
	November	0.05	16.60	35.30	25.95	45.00
	December	0.05	10.30	25.18	17.74	43.00
2020	January	0.00	08.80	28.50	18.65	56.00
	February	0.00	07.50	24.60	16.05	58.00
	March	0.00	10.40	26.50	18.45	60.00
	April	0.00	16.20	30.70	23.45	42.00
	May	0.00	24.50	38.60	31.55	51.00
	June	0.10	25.60	41.20	33.40	43.00
	July	0.00	24.30	45.50	34.90	42.00
	August	0.00	20.10	39.50	29.80	51.00
	September	0.00	18.10	40.50	29.30	54.00
	October	0.00	18.60	39.50	29.05	50.00
	November	0.00	14.50	32.70	23.60	51.00
	December	0.00	08.50	24.50	16.50	46.00

Source: Agro-Meteorological Center Tandojam. *R.H.= Relative humidity

Table 3. Mean squares of F_1 genotypes for yield and oil traits of sunflower grown under well watered and water stressed environments

Characters	Mean squares					
	Replication (R)	Genotypes (G)	Crosses (C)	Parents (P)	C *VS* P	Error
	D.F= 3	D.F=22	D.F=14	D.F=7	D.F=1	D.F=66
Days to seed formation	2.48	122.92**	105.32**	105.38**	492.13**	1.89
Plant height	55.77	773.58**	757.98**	902.39**	90.43**	36.86
Seed yield (kg ha^{-1})	488	119035**	168795**	21476.3**	2633.97**	788
Chlorophyll content	0.13	252.94**	149.88**	118.93**	398.51**	2.15
Linoleic acid	8.58	242.23**	294.51**	63.61**	760.64**	0.90
Oleic acid	3.70	64.99**	81.78**	11.84**	202.00**	0.95
Oil content	1.58	36.82**	19.10**	20.60**	398.51**	0.87
Protein content	2.15	32.95**	33.26**	3.78**	232.76**	1.15

**,* = significant at 1 and 5% probability level respectively

Results and Discussion

The foremost breeding aim of sunflower breeding is to evolve hybrids possessing higher grain yields, resistant to diseases and lodging along with good oil quality (21). By discerning CMS lines (22) and restorer genes (23), sunflower breeding for hybrid evolution was put in track very sparingly.

Contrary to heterosis, inbreeding depression is also a widespread manifestation in plant inhabitants; thus it is indispensable to discover genetic make-up that can guide fitness of parents and cross-breeding parents. The estimates of heterosis and inbreeding depression disseminate knowledge regarding gene action involved and cause their effect yield, oil and protein contents. Hence, present study was conducted to assess the level of the heterosis and inbreeding impact in 15 hybrids of sunflower in F_1 and F_2 generations correspondingly. It was stated that the effect of selection and impact of genetic components to explain inbreeding impact are somewhat multifaceted (24). If selection effect of homozygosity is small, then offspring created by autogamy will have low disadvantage. Inversely, homozygous setback is high; virtually any matting scheme will lead to be deleterious effects. The crossing due to additive type of genes may be suitable if on the contrary dominant genes produce high inbreeding effect (25). Stumpy inbreeding impact for different characters designated that such hybrids somehow favor the effectiveness of F_2 sunflower hybrids (26). The results regarding heterosis (Table 7) and inbreeding depression in sunflower are presented (Table 8, 9) for traits under investigation.

Days to seed formation

Early seed formation requires negative heterotic estimates to be beneficial. The heterotic effects concerning days to seed formation is cited in Table 4 showed that 4 F_1 hybrids articulated desirable negative relative heterosis that varied from -0.12 to -1.95% and heterobeltiosis from -0.66 to -8.47% in normal irrigation while other 11 hybrids in non-stress and 10 hybrids in stress exhibited undesirable positive relative and better parents heterosis. Nonetheless, F_1 hybrids like Mehran × Peshawar-93 and Mehran × UC-666 produced highest negative mid parent heterosis while Mehran × UC-666 expressed highest better parent heterosis followed by Mehran × Peshawar-93 in non-stress conditions. While F_1 hybrids like Mehran × Peshawar-93 revealed highest negative mid parent and high parent heterosis in optimum irrigation (Table 4). F_1 hybrids like PSF-025 × Peshawar-93 and Mehran × UC-666 established greater advantageous negative parental average heterosis and heterobeltiosis in both the environments (27) obtained positive and negative heterosis in the various hybrids nonetheless majority of the mid and better parent heterosis for maturity period was negative, that shown prompt maturity and earlier in seed formation can be achieved in sunflower hybrids.

It is commonly predicted that hybrids those manifest more vigour in F_1 hybrids also express high inbreeding depression in F_2 towing to loss of advantageous dominant genes, accumulation of harmful recessive genes and reduction in heterozygosity. F_2 hybrids with high negative inbreeding depression may be rewarding for early seed formation and eventually for early maturity**.** Seven F_2 progenies displayed positive inbreeding depression in non-stress and 4 in water stress conditions, while 8 F_2 progenies recorded desirable negative inbreeding depression in non-stress (Table 8) and 11 in stress environments (Table 9). The F_2 hybrids like Thatta × Peshawar-93, SH-3915 × UC-666 and Thatta × UC-666 showed maximum positive yet unadvantageous inbreeding in non-stress. Nevertheless the highest negative but desirable inbreeding depression was expressed by Thatta × B-2, followed by HO-1 × Peshawar-93, Mehran × B-2 and SH-3915× UC-666. Whereas maximum positive inbreeding depression were depicted in F_2 progenies like Thatta × UC-666 followed by HO-1 × B-2 and Thatta × Peshawar-9 in stress conditions (Table 9). These are preferable hybrids for exploitation and to develop early maturing F_2 hybrids. It was also noted that for days to seed formation, S1 lines ranged from 78.00 to 89.33 with an average of 84.99 days compared to average of base population Giza102 which formed seeds after 82.33 days (28).

Plant height

Medium plant height in sunflower is thought appropriate which provides resistance to plants from lodging. Minimum negative heterosis for plant height is appropriate since shorter plants are expected to be resistant for lodging and attain short life cycle. Our results indicated that under non-stress, the negative mid-parent and better parent heterosis ranged from -6.03 to -14.33 and -0.15 to -19.20% respectively. The same range under drought stress was noted as ranging from -0.53 to -25.15 and -1.38 to -29.16 respectively. From 15 F_1 hybrids, seven crosses displayed appropriate negative parental average heterosis in optimal irrigation and 8 F_1 hybrids in drought stress conditions. For better parent heterosis under non-stress, 8 hybrids recorded negative heterotic effects and 11 F_1 hybrids in stress environment (Table 4). Nevertheless, the superior crosses Mehran × peshawar-93 and Thatta × Peshawar-93 created highest negative relative heterosis in normal irrigation, while in water stress, Thatta × Peshawar expressed maximum mid-parent and better parent heterosis. The next higher heterobeltiosis were exhibited by Thatta × B-2 and Thatta × Peshawar in non-stress respectively. Simultaneously Thatta × Peshawar-93 also demonstrated the maximum negative relative and high parent heterosis in both the environments. Two best hybrids Thatta × B-2 and Thatta × Peshawar that established higher yet valuable negative relative heterosis and heterobeltiosis in both the environments were recognized as involving parents with high × high and high × low impacts that advocated that additive × additive and additive × dominant genes were operating for the expression of heterotic effects in hybrids for plant height and such results indicated that hybrids involved additive and complementary gene interactions respectively. Our findings indicated that some hybrids expressed undesirable positive heterotic effects whereas others manifested desirable negative heterosis for plant height. Coinciding to these findings, it was also reported that some positive heterosis for plant height (29, 30). Still analogous to present outcomes, testified some negative heterosis for plant height (31), yet perceived both negative and positive parental average heterosis and high parent heterosis extended from -8.0 to 16% and -2.0 to 4% for plant height respectively (32-34). It was observed contradictory results and that their all 18 hybrids manifested positive mid-parent (MPH) and better parent heterosis (BPH) for the

Table 4. Heterosis of F_1 hybrids for days to seed formation and plant height of sunflower grown under well water and water stressed environments

F_1 hybrids	Days to seed formation			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	22.09	16.32	18.59	12.59
Mehran × UC-666	-0.68	-10.16	-0.66	-9.50
Thatta × UC-666	-0.12	-2.03	-6.99	-8.10
PSF-025 × UC-666	5.16	-2.35	0.17	-5.83
SH-3915 × UC-666	12.90	8.01	6.40	1.75
HO.1 × Peshawar-93	19.22	17.71	15.98	15.85
Mehran × Peshawar-93	-3.34	-7.36	-8.47	-12.27
Thatta × Peshawar-93	11.34	6.75	10.27	5.78
PSF-025 × Peshawar-93	-1.95	-3.37	-5.18	-6.06
SH-3915 × Peshawar-93	8.82	6.98	1.05	0.16
HO.1 × B-2	2.75	-0.03	-3.12	-6.06
Mehran × B-2	4.05	-4.00	0.03	-7.00
Thatta × B-2	16.71	16.44	13.41	13.41
PSF-025 × B-2	3.61	-1.81	3.73	-0.42
SH-3915 × B-2	12.49	9.91	9.10	6.59
F_1 hybrids	Plant height			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	12.69	11.16	6.56	5.35
Mehran × UC-666	-6.03	-14.13	-9.61	-17.76
Thatta × UC-666	-7.92	-17.47	-10.51	-20.13
PSF-025 × UC-666	19.63	15.35	8.33	4.20
SH-3915 × UC-666	4.71	2.11	7.66	-0.30
HO.1 × Peshawar-93	9.31	0.98	3.34	-3.93
Mehran × Peshawar-93	-14.33	-16.48	-16.62	-19.44
Thatta × Peshawar-93	-13.9	-17.78	-25.15	-29.16
PSF-025 × Peshawar-93	16.47	9.31	8.01	5.40
SH-3915 × Peshawar-93	3.46	2.17	2.59	1.01
HO.1 × B-2	0.47	-0.15	-1.27	-1.38
Mehran × B-2	4.28	-5.61	-5.38	-14.70
Thatta × B-2	-9.07	-19.20	-18.91	-28.28
PSF-025 × B-2	2.67	-2.00	-0.53	-5.27
SH-3915 × B-2	10.06	0.80	1.67	-6.73

plant height (27). The extent of MPH varied from 7.8 to 34.9% whereas BPH ranged from 24.6 to 100.2%.

Shorter plants are greatly associated with shorter duration. All the crosses showed negative inbreeding depression for plant height in both the conditions. The high but useful negative inbreeding depressions however were recorded in F_2 hybrids like SH-3915 × UC-666 (-16.50%), PSF-025 × UC-666 (-13.25%) and Thatta × UC-66 (-10.75%) in non-stress conditions (Table 8). Under stress conditions, desirable negative inbreeding depressions was also observed in hybrids PSF-025 × B-2 followed by SH-3915 × Peshawar-93 and SH-3915 × UC-666 (Table 8). The high inbreeding depression in negative direction can lead to develop F_2 hybrids with shorter plant height (26). Analogous to present findings (26) reported high inbreeding depression for plant height extended between -3% to -26% and that is the lowermost inbreeding despair designated high heterozygosity thus showed minor deprivation of dominant genes operated in F_2 populations. Reports are also on higher inbreeding depression, around 23% in 4 F_2 hybrids (26). These hybrids may suit better for short duration sunflower F_2 hybrids. From 24 S1 lines, it was noted that Only 9 S1 lines recorded significantly plant height compared with the base population of Giza102, however plant height of the 23 S1 varied from 128.67 to 201.00 cm with an average of 158.15 cm, compared to 153.67 cm for the base pop. Giza102, showing a small amount of inbreeding depression (2.92%) (28).

Seed yield (kg ha^{-1})

Under non-stress, top of 3 hybrids like HO-1 × B-2, Thatta × UC-666 and PSF-025 × B-2 recorded higher relative heterosis of 16.02, 12.29 and 7.42% and heterobeltiosis of 11.84 %, 8.94% and 7.32% respectively for yield kg ha^{-1}. The maximum mid parent heterosis was produced by the hybrid HO-1 × B-2 and next higher scoring was Thatta × UC-666 and 3rd was Mehran × Peshawar-93 in water stress conditions (Table 5). The cross Thatta × UC-666 was observed as having highest heterobeltiosis (16.73%) followed by HO-1 × B-2 (14.90%) and Mehran × Peshawar-93 (9.00%) in stress environment. At least 3 hybrids like Thatta × UC-666, HO-1 × B-2 and Mehran × Peshawar-93 were identified manifesting high parental mean heterosis and high parent heterosis in optimal and moisture scarce conditions. These hybrids were developed from the parents which used good × poor, good × good and good × good GCA inbreds. Such findings revealed that complementary interaction of genes

Table 5. Heterosis of F_1 hybrids for days to seed formation and plant height of sunflower grown under well water and water stressed environments

F_1 hybrids	Seed yield (kg ha^{-1})			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	-2.29	-2.31	-5.30	-5.36
Mehran × UC-666	-2.89	-6.81	-3.48	-5.49
Thatta × UC-666	12.29	8.94	17.58	16.73
PSF-025 × UC-666	-6.94	-10.20	-9.69	-13.63
SH-3915 × UC-666	-8.68	-10.78	-10.60	-11.17
HO.1 × Peshawar-93	-9.61	-12.68	-14.14	-15.82
Mehran × Peshawar-93	2.70	1.96	9.07	9.00
Thatta × Peshawar-93	-3.28	-3.68	-3.74	-5.01
PSF-025 × Peshawar-93	-10.13	-10.25	-3.34	-5.70
SH-3915 × Peshawar-93	-26.00	-12.95	-13.62	-14.84
HO.1 × B-2	16.02	11.84	17.93	14.90
Mehran × B-2	-1.53	-2.01	-5.76	-6.30
Thatta × B-2	-0.15	-16.28	-5.97	-7.79
PSF-025 × B-2	7.42	7.32	6.63	4.68
SH-3915 × B-2	-12.14	-13.33	-13.81	-15.56
F_1 hybrids	**Chlorophyll content**			
	Well watered		**Water stressed**	
	M.P. (%)	**B.P. (%)**	**M.P. (%)**	**B.P. (%)**
HO.1 × UC-666	6.44	4.39	40.33	19.87
Mehran × UC-666	29.94	19.94	88.31	64.45
Thatta × UC-666	43.10	36.81	88.19	62.5
PSF-025 × UC-666	-5.44	-14.32	21.02	-7.66
SH-3915 × UC-666	7.65	0.03	43.28	13.08
HO.1 × Peshawar-93	27.27	24.00	40.95	39.62
Mehran × Peshawar-93	65.75	59.75	73.61	67.61
Thatta × Peshawar-93	32.71	32.71	58.58	55.09
PSF-025 × Peshawar-93	-4.60	-8.07	20.83	6.13
SH-3915 × Peshawar-93	24.84	15.02	34.40	23.14
HO.1 × B-2	49.57	46.70	65.06	55.68
Mehran × B-2	33.57	23.29	44.19	32.72
Thatta × B-2	21.66	16.31	33.84	24.71
PSF-025 × B-2	24.10	12.44	34.68	23.75
SH-3915 × B-2	27.70	22.84	41.03	35.49

Table 7. Heterosis of F_1 hybrids for days to seed formation and plant height of sunflower grown under well water and water stressed environments

F_1 hybrids	Oil content			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	8.75	3.57	10.32	1.87
Mehran × UC-666	4.05	-2.97	0.52	-5.00
Thatta × UC-666	15.98	7.73	13.81	8.12
PSF-025 × UC-666	0.04	2.97	3.20	0.62
SH-3915 × UC-666	12.50	-1.78	-2.56	-5.00
HO.1 × Peshawar-93	12.13	11.76	12.87	8.10
Mehran × Peshawar-93	25.37	22.22	21.21	18.91
Thatta × Peshawar-93	9.05	5.88	8.21	6.75
PSF-025 × Peshawar-93	9.49	6.13	9.33	7.89
SH-3915 × Peshawar-93	4.45	1.86	4.00	2.63
HO.1 × B-2	21.68	19.07	23.47	20.19
Mehran × B-2	12.79	12.71	5.07	4.81
Thatta × B-2	10.49	9.96	5.88	5.55
PSF-025 × B-2	19.93	13.49	19.28	15.78
SH-3915 × B-2	10.27	4.96	3.01	0.00

F_1 hybrids	Protein content			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	-1.12	-3.29	-11.11	-13.92
Mehran × UC-666	-17.94	-19.58	-21.79	-25.60
Thatta × UC-666	-3.26	-8.24	9.45	9.45
PSF-025 × UC-666	-18.85	-19.31	-11.26	-14.86
SH-3915 × UC-666	-31.84	-33.69	-21.48	-28.37
HO.1 × Peshawar-93	-35.82	-37.50	-40.00	-40.74
Mehran × Peshawar-93	-4.66	-5.15	0.61	0.00
Thatta × Peshawar-93	-16.06	-16.49	-7.09	-11.11
PSF-025 × Peshawar-93	-27.17	-30.20	-19.46	-25.92
SH-3915 × Peshawar-93	2.12	0.00	19.71	4.93
HO.1 × B-2	-9.78	-10.75	-10.55	-12.19
Mehran × B-2	-12.63	-14.43	-7.31	-7.31
Thatta × B-2	-26.31	-27.83	-17.94	-21.95
PSF-025 × B-2	2.76	0.00	14.66	4.87
SH-3915 × B-2	-9.18	-9.67	-3.49	-15.85

in first hybrid and additive genes in second and third hybrids respectively were operating; hence hybrid development would be rewarding while single plant selection would be effective in early filial generations. Analogous to our results, reports are on the parental mean heterosis (up to 72%) and high parent heterosis (up to 57%) for seed yield (3). A broad array of heterosis for seed yield and oil quality traits in sunflower is observed by several previous researchers (35, 36). Some hybrids like CMS-XA × P124R, CMS-XA × P100R, PKU-2A × P124R, ARG-2A × P100R, ARG-3A × P124R, ARG-6A × P69R, DV-10A × P100R and PRUN-29A × RCR-8297 are identified with higher SCA effects for seed yield under both optimum and water stress environments (8). Upper edge heterosis for seed yield was also testified (7). Achene yield increased up to 14.21% over mid parent and up to 9.91 for better parent and up to 26.46% over standard check (37).

The harmful impacts of homozygosity in F_2 progenies are well recognized. Though whole set of 15 F_2 descendants verified negative inbreeding effects in both the environments, yet decrease in F_2 in either non-stress or in stress conditions was generally similar. The range of inbreeding effect in non-stress ranged from -2.59 to -23.71%

Table 8. Inbreeding depression in F_2 progenies of sunflower genotypes for various traits grown in well watered environments

F_2 progenies	DSF	PH	SYKH	CC	LA	OA	OC	PC
HO.1 × UC-666	-0.87	-6.39	-14.93	-1.05	-1.05	-1.48	-5.75	-2.27
Mehran × UC-666	0.77	-6.86	-18.50	-1.05	-0.97	-1.74	-6.75	-1.28
Thatta × UC-666	1.46	-10.75	-13.93	-6.83	-0.59	-1.44	-4.97	-2.25
PSF-025 × UC-666	-0.33	-13.25	-2.87	2.08	-1.05	-1.75	-5.20	-2.82
SH-3915 × UC-666	1.54	-16.50	-11.14	-3.92	-1.21	-2.06	-5.45	-1.64
HO.1 × Peshawar-93	-1.39	-2.37	-18.86	-5.99	-1.42	-2.00	-6.43	-1.67
Mehran × Peshawar-93	-0.81	-1.84	-3.64	-4.98	-0.86	-1.45	-8.02	-1.09
Thatta × Peshawar-93	1.66	0.47	-3.79	-1.18	-1.11	-1.92	-6.17	-1.23
PSF-025 × Peshawar-93	-0.66	-1.17	-19.31	-2.91	-1.38	-2.25	-2.89	-1.49
SH-3915 × Peshawar-93	1.23	-0.78	-2.59	-2.91	-0.65	-1.79	-4.88	-2.08
HO.1 × B-2	1.01	-1.90	-2.76	-10.11	-0.60	-1.45	-4.97	-1.20
Mehran × B-2	-1.72	-1.71	-22.94	-10.87	-0.93	-2.88	-2.44	-1.20
Thatta × B-2	0.92	-1.95	-5.22	-7.42	-1.28	-3.09	-5.00	-2.86
PSF-025 × B-2	-1.82	-3.52	-2.67	-7.94	-0.91	-1.49	-7.03	-2.15
SH-3915 × B-2	-1.85	-2.02	-23.71	-9.09	-1.37	-2.20	-7.69	-1.19

DSF= Days to seed formation, **PH**= Plant height, **SYKH**=Seed yield kg ha-1, **CC** = Chlorophyll content, **LA**= Linoleic acid, **OA**= Oleic acid, **OC**=Oil content, **PC**= Protein content

Table 9. Inbreeding depression in F_2 progenies of sunflower genotypes for various traits grown in water stressed environments

F_2 progenies	DSF	PH	SYKH	CC	LA	OA	OC	PC
HO.1 × UC-666	-1.30	-2.12	-19.03	-3.74	-1.49	-3.54	-4.29	-1.47
Mehran × UC-666	-1.41	-2.79	-14.93	-0.74	-1.74	-3.92	-2.63	-3.28
Thatta × UC-666	1.18	-2.38	-13.63	-4.45	-2.47	-2.38	-2.89	-2.47
PSF-025 × UC-666	-0.73	-1.65	-14.05	-0.52	-1.12	-3.26	-3.11	-1.59
SH-3915 × UC-666	-2.23	-4.83	-17.56	-0.46	-1.61	-3.49	2.63	-1.89
HO.1 × Peshawar-93	-2.29	-0.85	-6.71	-0.45	-1.54	-3.57	2.50	-2.08
Mehran × Peshawar-93	0.69	-2.09	-5.12	-0.38	-4.00	-1.57	2.27	-3.66
Thatta × Peshawar-93	0.88	-1.03	-4.93	-0.41	-1.28	-4.65	1.27	-2.78
PSF-025 × Peshawar-93	-1.11	-3.11	-14.84	-0.45	-1.49	-3.95	-4.88	-1.67
SH-3915 × Peshawar-93	-1.19	-5.06	-11.24	-0.77	-0.35	-3.85	-2.56	-3.53
HO.1 × B-2	1.06	-3.09	-3.85	-0.36	-0.31	-3.13	2.33	-1.39
Mehran × B-2	-2.29	-3.58	-6.39	-0.43	-0.98	-3.19	1.33	-3.95
Thatta × B-2	-3.77	-2.86	-5.43	-1.09	-3.89	-4.88	-2.63	-3.13
PSF-025 × B-2	-2.19	-5.09	-5.91	-6.15	-0.93	-1.61	0.00	-2.33
SH-3915 × B-2	-2.03	-3.75	-19.66	-4.17	-5.26	-10.14	-2.63	-2.90

in normal condition whereas same range in water stress was -3.85 to -19.66. The lowest range of inbreeding effect was nevertheless recorded in F_2 hybrids such as SH-3915 × Peshawar-93, PSF-025 × B-2, HO-1 × B-2, and PSF-025 × UC-666 in non-stress (Table 8). These consequences specified low magnitude of inbreeding effect and divulging the lower degradation of dominant or over-dominant type of genes engaged in this case. Reports are on the lower inbreeding may be attributable to close linkages between dominant and additive genes (26). The utmost susceptible hybrids with high inbreeding effects were witnessed in F_2 hybrids (SH-3915 × B-2) with depression values of -23.71% in non-stress condition. The highest magnitude of inbreeding depression (around -18%) was exhibited in crosses SH-3915 × B-2 followed by HO-1 × UC-666 and SH-3915 × UC-666 and lowest inbreeding depression (around 5%) was observed in HO-1 × B-2 followed by Mehran × Peshawar-93 and Thatta × B-2 in stress condition (Table 9). Low level of inbreeding impact (18%) was detected in cross HAR-5 × HAR-2, likewise cross RHA- 387 × RHA-859 exhibited 71% inbreeding effect for seed yield (38).

Chlorophyll content

The results concerning heterotic effects for chlorophyll content revealed that greater number of the hybrids created positive heterotic impacts under both the environments (Table 5) excluding few which documented negative heterosis for chlorophyll content. In non-stress, relative heterosis was recorded up to 65.75% and better parent heterosis up to 59.75%. Likewise the same range in drought stress was noted up to 88.31% (relative heterosis) and up to 67.61% (heterobeltiosis). The hybrids Mehran × Peshawar-93 expressed higher positive relative heterosis of 65.75% and heterobeltiosis of 59.75% yet another hybrid HO-1 × B-2 created fair amount of mid parent heterosis (49.57%) and heterobeltiosis (46.70%) in normal irrigation conditions. The extent of progressive heterosis was apparently higher under moisture shortage conditions which designated those hybrids expressed/triggered on added favourable genes under drought environment. The hybrids Mehran × UC-666, Thatta × UC-666 and Mehran × Peshawar-93 recorded maximum relative heterosis (88.31, 88.19 and 73.61%), while hybrids Mehran × Peshawar-93, Mehran × UC-666 and Thatta × UC-666 also gave higher (67.61, 64.45 and 62.5%) with little bit change in rank order also created higher better parent heterosis for chlorophyll content under stress conditions. The hybrids Mehran × Peshawar-93, Mehran × UC-666 and Thatta × UC-666 were developed from crossing the inbreds having good × good, good × poor and good × poor GCA parents suggesting that in first hybrid additive genes while in second and third hybrids, complementary genes with epistasis effects were functioning. Such results indicated that chlorophyll content can be improved through hybrids or single plant selection in segregating populations.

Except one in non-stress, all the F_2 progenies recorded negative inbreeding depression for the chlorophyll content up to -10.87% in normal conditions (Table 8), while the same range in drought stress was up to -6.15% (Table 9). The effect of inbreeding in drought was quite lower than the non-stress conditions. The elevated depression (around 10%) however were observed in F_2 progenies like Mehran × B-2, HO-1 × B-2 and SH-3915 × B-2 while the lowest inbreeding depressions were depicted by HO-1 × UC-666 and Mehran × UC-666 with equal depression of -1.05% under normal conditions. Results further revealed that highest inbreeding depression was shown by F_2 progenies PSF-025 × B-2, Thatta × UC-666 and SH-3915 × B-2, nevertheless minimum inbreeding depression (below 1%) was revealed by HO-1 × B-2 followed by Mehran × Peshawar-93 in stress conditions (Table 9). Small inbreeding depression for different characters specified that such hybrids somehow favor the efficiency of F_2 sunflower hybrids.

Linoleic acids (%)

Very few hybrids expressed positive heterotic estimates. The calculations concerning the heterosis for this character accessible in (Table 6) demonstrated that the highest parental mean heterosis (9.55%) and heterobeltiosis (7.78%) was created by the hybrid Mehran × Peshawar-93 whilst HO-1 × B-2 was next good ranker for only relative heterosis and Thatta × UC-666 ranked third with respect to relative and heterobeltiosis under normal irrigation. While in stress conditions, HO.1 × B-2, Mehran × Peshawar-93 and Mehran × UC-666 were among top three hybrids for relative heterosis (around 6%) and Mehran × Peshawar-93 and Thatta × UC-666 (around 4%) for better parent heterosis in stress conditions. From 15 F_1 hybrids evaluated, at least 2 hybrids such as Mehran × Peshawar-93 and Mehran × UC-666 were identified as manifesting high mid and better parent heterosis for linoleic acid in both the environments. Results indicated that both heterobeltiotic hybrids involved high × low parents revealing that complementary gene interactions supported the expression of high heterosis for linoleic acid content. Hybrid sunflower development is worth to be exploited. Contrary to our results, observations are on significantly negative parental mean heterosis for linoleic acid (up to -38.02%) and high parent heterosis (up to 66%) (3). Analogous to our findings, high heterotic estimates up to16.19% over mid parents and up to 20.66% over better parents were observed (35). They further noted maximum positive high parent heterosis for linoleic acid in hybrid TS-18 × TR-6023 (16.19%) and heterobeltiotic effect of linoleic acid was negative in nine F_1 hybrids that ranged from –20.66 to 9.69%. In a similar study, it was reported that positive heterosis in 28 F_1 hybrids over parental mean heterosis (39). The heterobeltiosis however ranged from 66.24% (A1 × Rf9) to 22.87% (A7 × Rf18) in both the hybrids.

It is polyunsaturated oil with low saturated fat content, a clean, light flavor with high vitamin E content. Similar to most of the characters, all the F_2 progenies recorded negative and lower % of inbreeding depression (up to 1.42%) in non-stress (Table 8). The maximum inbreeding depression (up to -1.38%) were noted in hybrids HO-1 × Peshawar-93, PSF-025 × Peshawar-93 and SH-3915 × B-2 in control conditions, while estimate of inbreeding depression was high for linoleic acid (around -4%) in SH-3915 × B-2, Mehran × Peshawar-93 and Thatta × B-2 under drought conditions. The negligible level of inbreeding effect was noted in HO.1 × B-2 followed by SH-3915 × Peshawar-93 and PSF-025 × B-2 in water stress conditions (Table 9). These outcomes showed low magnitude of inbreeding effect and revealing the minor deprivation of dominant dominant genes operating in F_2s.

Oleic acid

The results accessible in (Table 6) exhibited that the oleic acid showed a rational level of heterosis in fewer hybrids under regular irrigation conditions and water stress as well. The positive parental mean heterosis and high parent heterosis in non-stress and in well watered conditions fluctuated from 4.15 to 14.45% and 3.03 to 27.91; 3.07 to 12.09 and 2.00 to 27.27% respectively. The extent of heterosis in

Table 6. Heterosis of F_1 hybrids for days to seed formation and plant height of sunflower grown under well water and water stressed environments

F_1 hybrids	Linoleic acid			
	Well watered		Water stressed	
	M.P. (%)	B.P. (%)	M.P. (%)	B.P. (%)
HO.1 × UC-666	-7.14	-10.86	-7.58	-14.64
Mehran × UC-666	-2.86	-4.03	-7.39	-8.28
Thatta × UC-666	4.24	3.52	4.51	3.18
PSF-025 × UC-666	-13.47	-15.65	-16.56	-18.09
SH-3915 × UC-666	-13.44	-15.09	-22.50	-23.92
HO.1 × Peshawar-93	-32.03	-35.01	-30.85	-34.56
Mehran × Peshawar-93	9.55	7.78	7.26	5.51
Thatta × Peshawar-93	-17.07	-17.30	-22.18	-23.20
PSF-025 × Peshawar-93	-12.92	-14.77	-14.10	-17.79
SH-3915 × Peshawar-93	-6.62	-8.05	-8.33	-12.26
HO.1 × B-2	4.31	-3.44	9.73	-0.90
Mehran × B-2	-2.44	-7.18	-4.07	-7.27
Thatta × B-2	-7.48	-10.34	-11.00	-14.24
PSF-025 × B-2	-4.23	-5.40	-1.52	-2.12
SH-3915 × B-2	-14.78	-16.37	-18.90	-19.39
F_1 hybrids	**Oleic acid**			
	Well watered		**Water stressed**	
	M.P. (%)	**B.P. (%)**	**M.P. (%)**	**B.P. (%)**
HO.1 × UC-666	4.28	-3.57	6.60	-0.87
Mehran × UC-666	-6.08	-8.73	3.03	2.00
Thatta × UC-666	14.45	12.09	27.91	27.27
PSF-025 × UC-666	-8.39	-12.30	-10.24	-14.01
SH-3915 × UC-666	-17.24	-20.87	-15.68	-18.86
HO.1 × Peshawar-93	-22.77	-28.57	-22.93	-26.31
Mehran × Peshawar-93	12.65	9.52	24.50	22.11
Thatta × Peshawar-93	-14.40	-16.12	-15.27	-17.30
PSF-025 × Peshawar-93	-28.51	-31.53	-27.96	-28.96
SH-3915 × Peshawar-93	-10.15	-14.05	-0.95	-1.88
HO.1 × B-2	4.15	-1.42	23.07	12.28
Mehran × B-2	-17.13	-17.45	-3.09	-6.00
Thatta × B-2	-22.08	-22.40	-15.02	-17.17
PSF-025 × B-2	5.09	3.07	23.38	15.88
SH-3915 × B-2	-28.71	-30.17	-31.00	-34.90

drought stress was greater against normal irrigation. The F_1 hybrids Thatta × UC-666, Mehran × Peshawar-93 and PSF -025 × B-2 demonstrated the uppermost relative heterotic effects in both the environments. Likewise same F_1 hybrid created maximum heterobeltiosis effects in both the environments. From a total 15 F_1 hybrids evaluated for heterosis, at least 3 hybrids like Thatta × UC-666, Mehran × Peshawar-93 and PSF-025 × B-2 were located as having high relative heterosis and heterobeltiosis under both the environments. Such hybrids expressed high heterosis due to involvement of poor × good, good × poor and poor × poor GCA inbreds which indicated that in first 2 hybrids complementary genes and in third dominant genes were involved in the expression of high heterotic effects. Thus, all the three hybrids deserve the exploitation of hybrid sunflower development. Similar to present findings, reports are on the parental mean heterosis (40%) and high parent heterosis (38%) (3). In another study, (35) also verified parental mean heterosis (52%) and better parent heterosis (51%), nevertheless hybrid TS-335 × 291RGI exhibited maximum negative mid and high parent heterotic effects while hybrid TS-18 × R-25 expressed highest positive mid and high parent heterosis. Quite a higher was observed by (39) in their heterotic studies and noted the maximum heterosis

(39.59%) against parental mean heterosis (39%) over high parents.

All of the F_2 progenies showed low to moderate level of inbreeding impacts which varied from -1.44% up to -3.09% in non-stress (Table 8) and -1.57 to -10.14% under water stress conditions (Table 9). Inbreeding effect was higher in stress than in non-stress environments (Table 5). However, F_2 hybrids Thatta × B-2, followed by Mehran × B-2 and PSF-025 × Peshawar-93 exhibited around 3% depression, yet PSF-025 × UC-666 followed by Mehran × Peshawar-93 and PSF-025 exhibited around 1.5% but low inbreeding depression in non-stress conditions. While under stress conditions, the F_2 hybrids like SH-3915 × B-2 revealed high inbreeding depression followed by Thatta × B-2 (-4.88%) and Thatta × Peshawar-93 (around -6%) and lowest magnitude (around -1.5%) was exposed by Mehran × Peshawar-93 followed by PSF-025 × B-2 and Thatta × UC-666 in water stress conditions (Table 9).

Oil content (%)

Sunflower oil quality of is examined as the proportion of oleic: linoleic acid. The utmost fatty acid structure in sunflower oil is 55-65% of linoleic acid, 20-30% of oleic acid. In addition to agronomic and seed yield, oil quantity is also significant parameter for which sunflower is attractively grown. Sunflower is assumed as the supreme crop for amongst the edible crops which can effectively fulfill forthcoming oil necessity of the country. All the F_1 hybrids revealed positive parental mean and high parent heterosis excluding 2 hybrids which manifested negative better parent heterosis in non-stress while one negative relative and 2 negative high parent heterosis in moisture stress conditions (Table 7). These results indicated that heterosis breeding is very useful approach to evolve high heterotic hybrids. The crosses Mehran × Peshawar-93, HO-1 × B-2 and PSF-025 × B-2 gave higher relative heterosis in common irrigation conditions. The high heterosis in stress conditions were produced by the hybrids HO-1 × B-2, Mehran × Peshawar-93 and PSF-025 × B-2 for mid parent and better parent respectively (Table 7). From the present results, it is quite apparent that 3 promising hybrids such as HO-1 × B-2, Mehran × Peshawar-93 and PSF-025 × B-2 were developed from crossed which is consisted of good × poor, poor × poor and good poor GCA inbreds, thus suggested that high heterotic impacts were developed by complementary genes in first and third hybrids yet dominant genes were involved in second hybrid. Such results connoted that hybrid sunflower will be the big achievement for improving oil quantity. Similar to our findings, both negative mid and better parent and positive and negative better parent heterosis were manifested by the hybrids which indicated that the choice of hybrids could be exploited for higher oil quantity (27). Current research consequences are in accordance with those of (26), who detected heterotic effects over parental average and a high parent heterosis at greater amount of relative heterosis (194%) and 182% for heterobeltiosis in oil yield (kg/ha). Reports are also on upper most progressive heterosis over parental mean and high parent heterosis for oil yield (7). Similar findings are also reported highest relative parent heterosis by the cross A18.6×A14.1 while cross A18.6×A22 displayed maximum heterobeltiosis for oil quantity, yet maximum standard heterosis was presented by A22×A2.5 for oil quantity (7, 37). The oil quantity up to 19.0% over mid parent, up to 17.2% over better parent and up to 36% over commercial check were reported.

Oil quantity is a polygenic trait, controlled by hundreds of trivial genes with small impact; henceforth low inbreeding effect is estimated. All the F_2 progenies recorded low negative inbreeding effect in non-stress conditions for oil content that varied from -2.44 to -8.02% in normal irrigation (Table 8) and some F_2 progenies recorded positive hence no inbreeding effects under water stress (Table 9). The hybrids which gave minimum or no inbreeding effect may be exploited for F_2 hybrids and these hybrids may possess additive genes which showed lower degradation and maintained heterozygosity to certain level. However, the F_2 hybrids such as Mehran × peshawar-93, SH-3915 × B-2 and PSF-025 × B-2 recorded maximum inbreeding depression (around 6% on average of 3 hybrids) for oil content in non-stress, whereas F_2 progenies SH-3915 × UC-666 followed by HO.1 × Peshawar-93 and Thatta × Peshawar showed no inbreeding depression in water stress conditions. It was stated that oil quantity being a multigenic character is advocated by trivial genes; consequently nethermost inbreeding influence is predicted (26).

Protein content (%)

Results produced in (Table 7) indicated that protein content showed rational heterosis in number of crosses under optimal irrigation as well as under drought stress conditions. The hybrids like PSF-025 × B-2 and HO-1 × B-2 expressed higher relative heterotic effects in optimum irrigation**.** Among the F_1 hybrids, the top three hybrids like SH-3915× Peshawar-93, PSF-025 × B-2 and Thatta × UC-666 scored maximum mid parent heterosis (up to 15% on average of 3 hybrids), while Thatta × UC-666, SH-3915 × Peshawar-93 and PSF-025 × B-2 exhibited high heterobeltiosis (up to 6% on an average of these 3 hybrids) under water stress environment (Table 7). The best 3 hybrids Thatta × UC-666, SH-3915 × Peshawar-93 and PSF-025 × B-2 which manifested higher parental average and heterobeltiosis used the inbred parents as good × poor, poor × poor and poor × good GCA parents revealing that second hybrid involved non-additive genes whereas first and third hybrids used complementary gene interaction in the expression of high heterotic effects for protein content. It was found that some hybrids which contributed dominant genes in the expression of heterosis for protein content (37). Reports are on 5 paramount hybrids with higher heterotic estimates. In case of parental mean, 4 hybrids were identified from their study (26).

Inbreeding depression was observed in all F_2 progenies in both non-stress and water stress conditions, thus drop in protein content from F_1s to F_2s was obvious (Table 8, 9). Inbreeding depression in F_2 hybrids varied from -1.09 to -2.86% and -1.39 to -3.95% in water stress conditions. High inbreeding depressions were observed in Thatta × B-2, PSF-025 × UC-666 and HO-1 × UC-666 with depression values of -2.86, -2.82, and -2.27 respectively, whereas the lowest inbreeding depression was noted in SH-3915 × B-2 (-1.19%) in normal conditions (Table 8). Mehran × B-2, Mehran × peshawar-93, and SH-3915 × peshawar-93 were F_2 hybrids that showed high inbreeding depression, with depression % of -3.95%, -3.66% and -3.53% respectively under drought stress. In stress condition, F_2 HO.1 × B-2 had the lowest inbreeding depression with a value of -1.39% (Table 9). Our results show lower range of inbreeding effects which are contradictory to the findings of (26) who observed the inbreeding effects in F_2 ranged from -19.18 to -14.33% whereas, present inbreeding depression varied from -109 to-2.86% in normal and -1.19 to -3.96% in water stress conditions.

Conclusion

Among the F_1 hybrids, 3 hybrids like Thatta × UC-666, Mehran × Peshawar-93 and HO.1 × B-2 showed high heterosis for majority of the traits in normal and adverse conditions may be recommended for further commercial exploitation. The F_2 progenies manifested high inbreeding depression for all the studied traits.

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Authors contributions

MHK conducted the experiment and wrote the paper, WAJ supervised the experiment and analyzed the data, MB and QDC helped in writing the research paper.

Compliance with ethical standards

Conflict of interest: No conflict of interest.

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